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2018

Ungar , P S , Healy , C , Karme , A , Teaford , M & Fortelius , M 2018 , ' Dental topography and diets of platyrrhine primates ' , Historical Biology , vol. 30 , no. 1-2 , pp. 64-75 . https://doi.org/10.1080/0891296

http://hdl.handle.net/10138/308901
https://doi.org/10.1080/08912963.2016.1255737

unspecified
submittedVersion

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Journal:	*Historical Biology*
Manuscript ID	Draft
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Ungar, Peter; University of Arkansas Fayetteville, Anthropology Healy, Carrie; University of Arkansas Fayetteville Karme, Aleksis; Helsingin yliopisto Matemaattis-luonnontieteellinen tiedekunta Fortelius, Mikael Teaford, Mark ; Touro University
Keywords:	New World monkeys, Teeth, Food

Dental topography and diets of platyrrhine primates

by

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Acknowledgements: We thank curators at the Museum of Comparative Zoology in Cambridge, MA, The Field Museum of Natural History in Chicago, the American Museum of Natural History in New York, the US National Museum of Natural History in Washington, DC, and the Museu Paraense Emilio Goeldi in Belém, Brazil for access to specimens in their care and their hospitality during our visit. Three of us (PSU, MF, MFT) were fortunate to have interacted with Percy Butler. He and his many works were inspirational to generations of dental researchers, and his legacy will remain with discipline for generations to come.

Funding Agency: LSB Leakey Foundation

ABSTRACT

More than half a century ago, Percy Butler (1963: 4) wrote that we "need to study the functions of teeth more thoroughly so as to be in a position to assess the adaptive significance of observed variations and their possible selective value". There have been many advances in the study of dental functional morphology since that time. Here we review the various approaches to characterizing and comparing occlusal form that have been developed, especially dental topographic analysis. We also report on a new study of dental topography of platyrrhine primates (n = 341 individuals representing 16 species) with known differences in both dietary preferences and other food items eaten. Results indicate frugivores, gummivores, folivores, and seed eaters each have a unique combination of slope, relief, angularity, sharpness, and occlusal patch size and count values. Likewise, among frugivores, those that supplement their diets with hard objects, insects, leaves, and seeds, also each have a distinctive suite of topographic features. We conclude that both primary and secondary diet choices select for occlusal form, and that functional morphology more reflects the types of foods and mechanical challenges they pose rather than the frequencies in which they are eaten.

KEY WORDS

New World monkeys, teeth, food

That teeth are adapted to diet is undeniable when specialized feeders, such as the Felidae and the vampire bat, have distinctive dentitions, or when dental divergence within a family, as between frugivorous and insectivorous phyllostomatid bats, is related to dietary differences. It is less clear how far the smaller differences between related species can be explained this way.

Butler, 1983: 289

1. Introduction

Percy Butler (1983) recognized that dental functional morphology in mammals reflects diet, and holds the potential to teach us something about the selective pressures involved in evolving that morphology. But while the differences between cats and bats are obvious, the subtler variation between closely-related species may be less so. When Butler wrote those words, dental functional morphology work on mammals, especially primates, had already shown great promise (Kay 1975, Rosenberger and Kinzey 1976, Seligsohn and Szalay 1978). Those that habitually consumed fruits, for example, had shorter molar shearing crests than those that preferred leaves or insects. But such studies were still in their infancy, and quantitative characterization was limited mostly to studies of crest lengths on unworn teeth. The ultimate potential of occlusal morphology to reveal subtle details about the diets to which species were adapted was yet to be established.

Work continued over the years that followed, and has recently accelerated, to better characterize the functional aspects of molar form in mammals. The idea has been to push the limits of what we can learn from the form-function relationship. Here we report on recent work in this vein, focusing on one of Butler's favorite target orders, Primates (Butler 1963). We review recent dental topographic analyses of occlusal form, and report on a large sample of new data collected from closely-related New World monkeys that demonstrate the potential of this approach to reveal functionally

relevant aspects of morphology related both to primary (= preferred) and secondary (= less commonly eaten) diet elements.

1.1 Background

To understand relationships between occlusal form and function, we must appreciate that mammalian cheek teeth work on two distinct levels at a time. At one scale, they are guides for chewing motions, but at a finer one, they are tools for fracturing foods. The two levels or scales at which teeth operate correspond roughly to what Butler (1983) called "internal" and "external" environments.

Simpson (1933) worked out the basic model for teeth as guides for chewing. He believed that chewing motions depended on the way teeth fit together in occlusion, which in turn depended on the shapes of molar crowns. He contrasted vertical and horizontal motions, and teeth with opposing crests with those with cusps and basins. He used the term *shearing* to describe vertical movement of crests sliding past one another, *grinding* to refer to horizontal movement of cusps sliding across basins, and *opposition* for movement of cusps into basins (today we call this *crushing*). He also linked these motions to diet by relating shearing to meat-eating, grinding to plant-eating, and opposition to a combination of the two. Crompton and Hiiemae (1970) and others began to work out the details of jaw movements and their relations to tooth form with cineradiographic studies of opossums in the late 1960s. Vertical movements, combined with steep crests or edges of contact running parallel to the plane of motion, allow opposing teeth to slide past one another with an action reminiscent of a pair of shears in action. When vertical movements are combined with broad cusps and deep basins perpendicular to the plane of motion, the result is crushing. Finally, when shearing and crushing components are combined, like with small crests or lophs on a horizontal surface, we get grinding.

But teeth are more than mere passive players in the game of mastication (*sensu* Hiiemae 1967). Peter Lucas (2004) has championed the idea of teeth as complex tools selected to fracture foods. Some foods are hard, and require high stress to initiate cracks in them. Others are tough, and demand significant work to spread those cracks to fragment food items. Chewing can be thought of as a perpetual death match in the mouth, with foods evolving ways to toughen or harden their tissues to resist fracture and teeth developing structures to overcome those defenses without themselves being broken in the process (Ungar 2008). A hemispherical cusp is well suited for initiating fracture in hard foods. It concentrates force on a small area, but at the same time, its bluntness protects the tooth from cracking. Because hard foods are often brittle, once a crack starts, it tends to spread easily. Opposing blades, on the other hand, are better suited for fracturing tough foods. Cracks spread with tension as they are wedged apart at the advancing tip. Those blades can be narrow since breakage is less of a concern when soft, tough items deform around tooth tissues (Lucas 2004, Ungar and Lucas 2010).

1.2 Characterizing occlusal functional morphology

In order to use dental functional morphology to infer diet in fossil taxa, it is important to develop standards for the quantitative characterization of occlusal form. Researchers have developed a number of approaches. The simplest approach is to count the number of cusps and lophs, or shearing blades, on a molar's surface (Liu et al. 2012). This, along with tooth height, can give us a pretty good sense of diet for many mammalian species. And when we add cusp shape and crest orientation to define specific crown types, we can get even more (Jernvall et al. 1996). Alternatively, we can measure areas of shearing and crushing on a tooth, and consider the

ratio of one to the other to gauge the relative importance of each to dental function (Friscia et al. 2007, Herring 1993, Janis and Fortelius 1988, Kay 1975, Sanson 1989).

The "gold standard" for primate studies has been Kay's (1984) shearing quotient analysis. The summed length of mesio-distal crests on a molar are plotted against tooth length for related species with diets judged similar, and a regression line is used to identify the relationship. The SQ is a measure of the deviation from that line, and indicates whether a species has longer or shorter crests than expected for that group. Folivorous and insectivorous primates tend to have higher SQs, and longer crests, than expected for a soft-fruit eater; and among frugivores, hard-object feeders tend to have the lowest SQ values, and bluntest cusps (Anthony and Kay 1993, Kay and Covert 1984, Meldrum and Kay 1997, Strait 1993).

But such studies are limited to unworn, or nearly unworn, teeth because they rely on landmarks that change or are obliterated with wear. This presents a problem because teeth begin to wear as soon as they come into the mouth, and natural selection must surely act to keep teeth functionally efficient as they wear. Indeed, many mammals exhibit what Fortelius (1985) called "secondary morphology"; they must wear to develop the sharp edges between softer dentin and harder enamel needed for food processing. Consider the guinea pig, for example, which actually grinds its teeth in utero so that they are worn and ready for use at birth (Teaford and Walker 1983). Unless we can characterize worn tooth morphology, we stand to lose an important part of the story -- how wear sculpts occlusal surfaces in a manner that promotes functional efficiency.

Some researchers (e.g., Seligsohn 1977, Teaford 1983) attempted to deal with worn teeth after the classic papers of Kay (1975, 1977) and Rosenberger and Kinzey (1976), but progress was limited by either the qualitative nature of the data or the technology available at the time. This began to change in the early 2000s, however, when dental topographic analysis was

developed as a landmark-free solution to the worn tooth conundrum (Ungar and M'Kirera 2003). It involves quasi-3D[1] characterization of whole occlusal surfaces, which offers the advantage of independence from human decisions as to what is important to measure. First, x,y,z points representing the occlusal surface of a tooth are collected using a laser scanner, touch-probe scanner, micro-CT scanner, or another instrument, and converted to a digital elevation model, or DEM (see Evans 2013, Ungar 2015 for review).

One approach to analyzing the resulting DEMs is by standard geographic information systems (GIS) measures, such as the first derivative of elevation (slope), the second derivative of elevation (slope of slope, or angularity), and ratio of 3D surface area to planimetric area (relief) (M'Kirera and Ungar 2003, Ungar and M'Kirera 2003). And results to date on a rather limited number of primate species confirm that folivorous taxa have more occlusal relief and more sloping, angular surfaces than do frugivores, and that among frugivores, hard-object feeders have the least slope and relief. Angularity also separates taxa, and appears rather insensitive to gross wear, at least to the point of dental senescence, when enamel is essentially worn away from the occlusal table and little occlusal relief remains. This means that, while teeth of most primate species get flatter with use, differences among taxa hold at comparable wear stages.

Other measures have been developed specifically with occlusal functional morphology in mind. These include optimal patch count rotated (OPCR) (Evans and Jernvall 2009) and Dirichlet normal energy (Bunn et al. 2011). Optimal patch count characterizes crown complexity as the number of contiguous areas of similar aspect (called *patches*) grouped by the four cardinal and four intercardinal directions. These patches have been likened to tools, with each viewed as

[1] These models are technically quasi-3D or 2.5D. While they are represented as a cloud of points with x, y, and z coordinates, they're not truly 3D because surface elevation is not independent of the horizontal coordinate axes – there is only one z-value possible for a given x-y pair (Turner, 1997).

a separate surface for processing food, and herbivores with tough, fibrous diets indeed tend to have higher values compared with carnivores. This approach has also proven valuable for distinguishing among living and fossil primates (Boyer et al. 2012, Boyer et al. 2010, Godfrey et al. 2012, Ledogar et al. 2013). And OPCR appears to be rather insensitive to phylogeny and gross differences in morphology. Dirchlet Normal Energy, in contrast, measures surface curvature using tools from differential geometry. It also separates primates by diet, as teeth with taller, sharper cusps have higher values (Winchester et al. 2014).

1.3 Primary and secondary food preferences and dental functional morphology

Despite the variety of analytical approaches developed, the number of studies of primate dental topography have remained limited, and the ultimate resolution of this approach for detecting subtle differences in diets is still unknown. For example, two primate species might both prefer ripe, fleshy fruits, but supplement their diets differently, say with leaves in one case and insects in another. It has often been assumed that preferred foods, or at least those most commonly eaten, have the greatest selective influence on molar design (Kay 1975), but as Kinzey noted for *Callicebus moloch* and *C. torquatus*, while both are primarily frugivorous, the former have longer shearing crests for slicing leaves, and the latter have a larger talonid basin for crushing insect chitin. Kinzey (1978: 378) intuited from this that, "when a food item is critical for survival, even though not part of the primary specialization, it will influence the selection of dental features".

This notion has developed into the idea of the fallback adaptation. Many primates have a penchant for succulent, sugar-rich foods, a legacy of the ancestral anthropoid dietary adaptation (Ross 2000, Ungar 2009). But differences in diet often emerge, hinging on seasonal shifts to

fallback foods taken when preferred resources are less available. In such cases, favored foods are easy to consume and digest, offer a low cost-benefit ratio, and may not result in selective pressures that would tax functional morphology. On the other hand, less desirable fallback foods might require some morphological specialization, even if those foods are only critical when preferred ones are unavailable (Robinson and Wilson 1998). One extreme example is *Lophocebus albigena* at Kibale in Uganda. This mangabey prefers soft, fleshy fruits, which it eats most of the time. But it falls back on hard seeds and bark when the forest is severely stressed, such as occurs during extreme El Niño events (Lambert et al. 2004). In this case, flat teeth and thickened crown enamel are needed only once-in-a-generation, but they still confer an advantage to those that have them.

But primate dental-dietary adaptations are complicated. Yes, some species have dental specializations for foods other than their preferred diets. But for other primates, mechanically challenging foods are the preferred ones. Consider another flat-toothed, thickly-enameled mangabey, *Cercocebus atys*, in the Ivory Coast's Taï National Park. The most abundant item in its diet is the *Sacoglottis* nut, which harder than a cherry pit (McGraw et al. 2014). *Cercocebus atys* specializes on these nuts because they are rot-resistant and available year round. Moreover, other primates are not dentally equipped to handle them.

In terms of selection for dental form then, as Butler (1983: 289) noted, "the ability to exploit an unusual food source in times of scarcity may be decisive." So can dental topography reflect both preferred foods and fallback ones? And can we parse the topography related to primary and secondary diet types? Here we provide an example of molar functional morphology of closely-related platyrrhine primates to begin to address these questions. We consider a large

sample of teeth representing 16 species in 11 genera, selected because of variation in both their primary food preferences, and their secondary diet choices.

2. Materials and methods

This study involved the characterization and analysis of crown topography of upper second molars (M^2s) of 341 wild-caught individuals from northeastern Brazil. The taxa, sample sizes for each, and their reported diets (both primary and secondary) are presented in Table 1. *Aotus*, *Ateles*, *Callicebus*, *Cebus*, *Lagothrix*, *Saguinus*, and *Saimiri* all prefer fruits, *Callithrix* consumes mostly gums, *Alouatta* eats more leaves, and *Pithecia* and *Chiropotes* favor seeds. Moreover, secondary diet items vary among the frugivores, with *Aotus*, *Saguinus* and *Saimiri* generally consuming more insects, *Ateles* more seeds, *Callicebus* and *Lagothrix* more leaves, and *Cebus* more hard objects (see Table 1 for references). Of course, all diet categories have shortcomings. For instance, some foods may be eaten frequently at some sites and less frequently at others (e.g., differences in proportion of leaves eaten by some groups of *Aotus*). Likewise, some categories may include foods with similar properties. For instance, hard objects and seeds can be overlapping categories, but we distinguish them here on the basis that *Cebus apella* typically consumes more hard-shelled seeds than do *Ateles* spp. For that matter, *Pithecia* and *Chiropotes* typically husk hard-shelled seed pericarps with their front teeth, so that molars can focus on the softer endocarp within (Norconk 2007, Rosenberger 1992). Thus, the purpose of these analyses is to give a first approximation of the usefulness of these techniques in making finer resolution functional distinctions between taxa.

Specimens used in this study are housed in various museum collections, including the Museum of Comparative Zoology in Cambridge, MA, The Field Museum of Natural History in Chicago, the American Museum of Natural History in New York, the US National Museum of

Natural History in Washington, DC, and the Museu Paraense Emilio Goeldi in Belém, Brazil. High-resolution impressions were taken of each primate dentition using President's Jet regular-body polyvinylsiloxane dental impression material (Colténe-Whaledent, Corp., Mawah, NJ), and replicas were poured using Epotek 301 (Epoxy Technologies, Inc., Billerica, MA) epoxy resin and hardener. The replicas were then coated with a thin layer of graphite (The B'Laster Corp., Valley View, OH) followed by Teflon (CRC Industries, Warminister, PA) to mitigate effects of translucency of the resulting casts during laser scanning. Replicas were mounted in putty on a horizontal plate so that the occlusal plane of the tooth row was as parallel as possible to the plate. A quasi-3D point cloud representing each occlusal surface was created using an XSM multi-sensor scanning machine (Xystrum Corp., Turino, Italy) with an integrated OTM3 laser head (Dr. Wolf & Beck GmbH, Wangen, Germany). Elevation data were collected at a lateral point spacing of 25 µm, resulting in a matrix of 1,600 z-values for each 1 mm^2 of tooth surface in the x-y plane.

Point clouds were then converted to ASCII format using Digiline software (Xystrum Corp., Turino, Italy) and processed using ArcGIS 10.2 (ESRI Corp., Redlands, CA). Digital elevation models of the surfaces were interpolated in ArcGIS using the inverse distance weighting, and cropped to include only the occlusal table, defined by elevations above the lowest point on the occlusal basin (see Klukkert et al., 2012 for details). The resulting surface models were characterized quantitatively using six variables: slope, angularity, relief, OPCR, patch size, and sharpness.

The first three variables considered were average surface ***slope*** (the first derivative of elevation), ***angularity*** (average slope of slope, or second derivative of elevation), and ***relief*** (the ratio of surface area calculated from triangulated irregular network models divided by the

underlying planimetric 2D areas). These measures are described in detail in Ungar and M'Kirera (2004) and M'Kirera and Ungar (2004), and were calculated in ArcGIS 10.2. The fourth variable, ***OPCR*** (orientation patch count, eight rotations) was calculated in SurferManipulator (Alistair Evans, 2008) as the number of contiguous patches of similar aspect taken in each of the four cardinal and four intercardinal directions, and averaged (Evans, Wilson, et al. 2007). Point clouds for each tooth were reduced to 50 data rows following standard protocol. The fifth variable, median ***patch size***, is the median of OPCR patch size in pixels, calculated in SurferManipulator. And the sixth variable, surface ***sharpness***, was calculated according to the GISWear method (Karme et al. 2010) as the areal proportion of steeply sloped elements to the rest of the surface (with shallower slopes), determined using the natural breaks method classification (Jenks' optimization) with three classes in ArcGIS 10.0. These attributes in combination provide a robust characterization of molar occlusal table morphology that reflects both surface complexity and relief.

In addition, each specimen was scored for gross wear using a modified version of Scott's (1979) method. Scott scores (0 to 10) were recorded for each cusp of each tooth, then the values were averaged, rather than summed, because *Callithrix* and *Saguinus* have three molar cusps, whereas the other taxa have four. We then divided individual specimens for each genus into three wear stages (1 = slight, 2 = moderate, 3 = extreme) for statistical analyses. The dividing line between the wear stages was set separately for each genus so as to assure as equal sample sizes as possible for each wear stage in the statistical analyses.

Principal components analysis (PCA) was used on the correlation matrix for all six variables to visualize patterns of specimen distribution in a low-dimensional space given that the variables are clearly not entirely independent of one another. Specimens were plotted by both

primary and secondary diets. Secondary diet comparisons were limited to taxa that consumed fruit as their primary diet, as the other primary diets were represented by only a single secondary diet type each. Second, two-factor multivariate analysis of variance (MANOVA) models, with diet and wear category as the independent variables and the six shape attributes as the dependent variables, were used to assess effects of food preference, dental wear, and the interaction between the two. Primary and secondary diet tests were conducted separately rather than by a nested model because, again, only frugivores had more than secondary diet represented. Data were rank transformed to mitigate violation of assumptions inherent in parametric statistics (Conover and Iman, 1981), and all six variables were included in the analyses. Single-classification ANOVAs on each variable and pairwise comparisons tests were used as needed to identify sources of significant variation. Both Tukey's HSD post hoc and Fisher's LSD a priori tests were used to balance risks of Type I and Type II errors (Cook and Farewell, 1996). Cases where Fisher's LSD test yielded $p < 0.05$ but Tukey's HSD test did not were treated as suggestive but of marginal significance.

3. Results

Summary statistics, considered by diet category and wear stage, are presented in Table 2.

3.1 Principal components analyses

Results from the principal components analysis show that PC1 and PC2 explain 45% and 30% of the variance respectively (Table 3). Component loadings indicate that sharpness, slope, angularity and relief variables contribute the most to PC1, whereas OPCR and patch size contribute the most to PC2 when all specimens are combined. Separate plots for each wear stage

evince good separation in PC1-PC2 bivariate space whether considered by primary diet or secondary diet for the frugivores (Figures 1-2). For primary diet variation, granivores separate well from gummivores and folivores along the PC1 axis, and frugivores and gummivores separate well from granivores and folivores along the PC2 axis. For secondary diets, among the frugivores, those that supplement with insects separate well along the PC1 axis from those that consume seeds and hard objects, with leaf-eaters occupying an intermediate space. These patterns hold for all wear stages.

3.2 General linear model for primary diet

The two-factor MANOVA with primary diet and wear as the independent variables yielded significant results for both attributes, as well as an interaction between the two factors (Table 4). Single-classifications ANOVAs on the primary diet x wear interaction was unable to detect significant variation in any individual variable, however, suggesting a low-level significance in multidimensional space; the result was clearly driven by the large number of degrees of freedom (df = 36, 1416). There was significant variation between groups considered by primary diet for all of the shape variables, and significant variation between groups considered by wear category for all but angularity and OPCR. Values for sharpness, slope, and relief generally declined with increasing wear, but angularity and OPCR values held steady.

Each of the primary diet groups has a distinctive suite of attributes that in combination separates it from the others. And all diet pairs differ significantly from one another in at least five of the six variables (Table 4). The frugivores, for example, have moderate but variable values for all attributes, suggesting moderate occlusal relief and fairly simple crowns (Figure 1). The seed eaters, in contrast, have less occlusal relief, with duller, less sloping crowns and smaller

patchs. Gummivores and folivores are at the opposite end of the spectrum, with higher average slope and other attributes -- relief and OPCR in the case of folivores, and sharpness and angularity for the gummivores.

3.3 Separating frugivores by secondary diet

The two-factor MANOVA with secondary diet for frugivores and wear as the factors also yielded significant results for both attributes (Table 5). In this case, though, there was no higher-order interaction between wear and diet. Single-classification ANOVAs revealed significant variation between secondary-diet groups for all of the shape variables and, once again, significant variation between groups considered by wear score for all variables except angularity and OPCR (these are reflected by the consistent patterns of differences across wear stages in the PC plots of Figure 2). As with the results for primary diet data, values for sharpness, slope, and relief generally declined with increasing wear, but angularity and OPCR values held firm.

Like the primary diet groupings, each secondary diet group for the frugivores also has a distinctive suite of attributes that separates it from the others. Pairwise comparisons tests show that pairs of secondary diet groups differ significantly by an average of more than four of the six attributes. Only one pair-wise comparison, hard-objects versus seeds, differs by as few as two attributes. Frugivores that supplement their diets with insects tend to have sharp, sloping cusps with high relief and angularity, but low OPCR values (Figure 2). Those that supplement with leaves also tend to have high angularity and relief, but high OPCR values and low patch sizes. In contrast, frugivores that supplement their diets with hard objects and seeds tend to have low angularity and relief values, in addition to low average sharpness and OPCR values respectively. And hard-object feeders tend to have larger patch sizes too.

4. Discussion

Results of this study make clear that platyrrhine dental topography reflects both the sorts of foods primates are adapted to eat, and the degree to which teeth are worn.

4.1 Wear-related changes to occlusal form

While wear-related differences in occlusal form are not the focus of this study, it should be noted that different topographic attributes responded differently to wear. First and foremost, none of the six variables showed interactions between wear and food type, either primary or secondary. This is important, because it suggests that differences in dental topography between diet types hold for any given stage of wear, so like-worn specimens can be compared directly to assess diet differences.

Furthermore, while most of the attributes changed with wear (e.g., more worn teeth were flatter, with less sloping surfaces and less topographic relief), two attributes, angularity and OPCR, did not differ significantly between the wear stages. In other words, while these variables separated groups by both primary and secondary diet, their values were relatively insensitive to wear. This is consistent with previous studies of both angularity and OPCR for a variety of primates (Cuozzo et al. 2014, Dennis et al. 2004, Evans, Fortelius, et al. 2007, Ungar and M'Kirera 2003).

Angularity and OPCR are both measures of complexity, or jaggedness, of the surface. And a lack of variation in complexity between wear stages has been argued to reflect the maintenance of a functional aspect of occlusal morphology with wear (Ungar and M'Kirera 2003). This

evidently relates to slope changes in the occlusal table resulting from angled walls of the pits that form as enamel gives way to softer dentin during tooth wear. The basic idea is that Nature selects for a spatial relationship between cap enamel and underlying dentin horns that allows wear to sculpt the teeth in a manner that maintains functional efficiency. This may be considered comparable to the phenomenon with herbivorous ungulate molars, which have complex infoldings and lophs that form sharp edges with dentin exposure for shearing and grinding tough vegetation. Indeed, surface complexity seems to hold steady for primate molars studied so long as there is some enamel remaining on the occlusal surface, after which jaggedness declines and functional senescence sets in (King et al. 2005).

4.2 Dental topography and diet

More to the point here, dental topography reflects diet in a manner that makes sense in terms of the biomechanics of chewing and food fracture. The frugivores, and especially the seed eaters, have fairly simple crowns and with low occlusal relief, and duller, less sloping crowns with smaller patches. This morphology is appropriate for pulping fruit flesh and crushing seeds. The folivores and gummivores are at the opposite end of the spectrum, with higher average surface slope for shearing tough foods. Of course, gums themselves aren't mechanically challenging, and likely put little selective pressure on the cheek teeth. But the secondary foods that *Callithrix* consumes, insects, have tough, chitinous exoskeletons most effectively pierced with pointed cusps or sharp occlusal blades (Crompton and Hiiemae 1970). While shearing and grinding tough, fibrous leaves is likely more efficient with *Alouatta* teeth given its higher OPCR values (and more "tools" for the job of food fracture), *Callithrix* benefits from more angular surfaces for piercing insect exoskeletons to release their contents.

The higher angularity average for *Callithrix* is more-or-less consistent with previous findings on strepsirrhine primates that insectivores have more curvature (i.e., higher Dirchlet Normal Energy values) than folivores (Winchester, et al. 2014). On the other hand, the observation that insect-feeding *Callithrix* had lower average relief and OPCR values than *Alouatta* runs counter to expectations given previous results on strepsirrhines (Boyer 2008, Bunn, et al. 2011). There are any number of possible explanations for the apparent discrepancy. It could be that in one case, (*Alouatta*), the tougher diet is the primary one while in the other (*Callithrix*), it is the secondary one. Or it could be as simple as the fact that we're considering very different primates here, and that phylogeny is confounding results. On the other hand, it does make some sense that the folivores would have more "tools" for food fracture than insectivores, as leaf eaters need to dice foliage to increase surface area for digestive enzymes to act on, whereas insect eaters must simply pierce, rupture, and separate chitinous exoskeletons to release the softer-tissue contents within (Lucas 2004, Prinz et al. 2003). A similar argument was used to explain higher optimal patch counts in herbivores as compared with carnivores (Evans, et al. 2007). Nevertheless, further study on more taxa should help resolve this.

Differences in molar functional morphology are also evident with subtler diet differences. When comparing platyrrhine frugivores, those that consume different foods as their secondary resources also differ significantly in their occlusal topography in predictable ways. As one might expect, those that supplement their fruit diets with insects and leaves have high angularity and occlusal relief. Further, secondary insectivores have sharper cusps but lower OPCR values than secondary folivores. And those that supplement with hard objects and seeds tend to have low angularity and relief values, as well as low average sharpness and OPCR values respectively. These attributes make sense given both food fracture properties and chewing biomechanics.

4.3 Selective influences on occlusal morphology

This also raises the important point that dental topography can reflect either preferred foods, less-commonly consumed items, or both (Ungar 2017). Debates concerning the relationship between proportion of a food type and its selective influence on molar design go back several decades (Kay 1975, Kinzey 1978, Rosenberger and Kinzey 1976). At first glance, it makes sense that more commonly eaten, and therefore presumably more important foods, should have a greater selective influence. But what about favored foods that are not protected against fracture by tough or hard tissues, like soft fruit flesh? These do not require specialized occlusal form. Some have argued, alternatively, that selective influence on tooth shape is proportional to the degree of mechanical protection of food rather than its frequency in the diet. Put another way, it doesn't matter what your teeth look like if you eat mush most of the time, but if have to chew rocks, even on rare occasion, to survive, then your teeth had better be able to handle rocks.

This may well explain the conundrum that Kay, Sussman and Tattersall (1978) encountered discovering that ring-tailed and brown lemurs had similar shearing crest lengths. Sussman (1977) had studied these species in three forest patches: one with brown lemurs but no ringtails, another with ringtails but no brown lemurs, and a third with both. The species overlapped in their diets (with both consuming fruits, leaves, flowers, and bark), but the brown lemurs ate more leaves, and the ringtails consumed more fruit. And this difference was consistent between sites and seasons, whether or not the same plant species were available at a given time and place. Sussman's observation was the inspiration for his species-specific dietary adaptations model, wherein "dietary patterns are ultimately dependent on the morphological and physiological adaptations of the species" (Sussman 1987: 152).

Kay and his colleagues proposed several possible explanations, one of which was the suggestion leaves may put stronger selective pressure than do fruits on shearing crest length. They mused, "how much folivory is needed to select for folivorous dental morphology?" (Kay, et al. 1978: 126). Could it be that shearing crest length doesn't reflect how many leaves you eat but, rather, whether you need to eat them at all? They had hit upon a profound and important new idea, though it would remain undeveloped for decades. This indeed can also explain why mangabeys at Kibale, which take hard food only at times of extreme resource stress, and those at Taï, which consume them more than any other food type, both have flat molar teeth with thick enamel (see above, and Lambert, et al. 2004, McGraw, et al. 2014). In the case of the mangabeys, as with the lemurs, it seems that selection is responding not to whether an animal prefers mechanically challenging foods, but to whether it needs to be able to eat them at all to survive.

A special example of this phenomenon is Liem's paradox. Consider Minkley's cichlid fish. Some have flat, pebble-like teeth adapted to crack hard snail shells; but these fish pass right by the snails when softer foods are available (Liem and Kaufman 1984). They avoid the very foods to which they are adapted given the choice. The paradox is, as Ichthyologist Karel Liem (1980) wrote, that "the most specialized taxa are not only remarkable specialists in a narrow sense, but also jacks-of-all-trades". So more specialized teeth can actually lead to broader, more generalized diets, at least when dental morphology does not limit the ability to consume preferred foods (Fortelius et al. 2014, Robinson and Wilson 1998).

Primates are no exception when it comes to fallback adaptations (Cuozzo et al. 2012). They tend to prefer soft, succulent, energy-rich fruit flesh to mechanically or chemically challenging foods. This is, as noted above, a legacy of the ancestral dietary adaptation (Ross

2000, Ungar 2009). Yes, there are examples where the most commonly eaten foods are hard or tough, like the *Saccoglottis* fruits taken by the mangabeys at Taï, or for that matter, the wild celery and other terrestrial herbaceous vegetation (THV) consumed by gorillas at Karisoke in Rwanda (Fossey and Harcourt 1977). And these primates have very specialized digestive anatomy to allow them to overcome the mechanical defenses of the plants they eat. It could well be the case, however, that these primates are not driven to eat mostly hard or tough foods because they prefer them, but rather, because availability demands it and their teeth allow it. In the case of the Taï mangabeys, niche partitioning with the many other primates in the forest evidently play a role in limiting their diets to items foraged mostly from leaf litter on the forest floor (McGraw 2007). While in the case of the Karisoke gorillas, hunting and forest clearing for firewood and cultivation around the Virunga Massif have kept the mountain gorillas to altitudes where little other than THV is available to eat (Mehlman 2008). Could these be examples of "perpetual" fallback feeders (Ungar 2004)?

Butler (1963: 4) wrote, "we have indeed made a beginning, but so far we have only scratched the surface, and our knowledge of the teeth of non-human primates is particularly superficial". While it's true that we still have much to learn about the relationships between dental form and function in primates, we've clearly come a long way in the past half century. Among the more important findings is that occlusal topography can teach us something about both primary and secondary dietary adaptations in primates.

References

Anthony MRL, Kay RF. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. American Journal of Science. 293A:356-382. Available from <Go to ISI>://A1993KR34200013

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. Journal of Human Evolution. 55(6):1118-1137. Available from http://www.ncbi.nlm.nih.gov/pubmed/18930306 doi 10.1016/j.jhevol.2008.08.002

Boyer DM, Evans AR, Jernvall J. 2010. Evidence of dietary differentiation among late Paleocene-early Eocene plesiadapids (Mammalia, Primates). American Journal of Physical Anthropology. 142(2):194-210. Available from <Go to ISI>://WOS:000277985400003 doi 10.1002/ajpa.21211

Boyer DM, Costeur L, Lipman Y. 2012. Earliest record of *Platychoerops* (Primates, Plesiadapidae), a new species from Mouras Quarry, Mont de Berru, France. American Journal of Physical Anthropology. 149(3):329-346. Available from http://www.ncbi.nlm.nih.gov/pubmed/22926965 doi 10.1002/ajpa.22119

Bunn JM, Boyer DM, Lipman Y, St Clair EM, Jernvall J, Daubechies I. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. American Journal of Physical Anthropology. 145(2):247-261. Available from http://www.ncbi.nlm.nih.gov/pubmed/21469070 doi 10.1002/ajpa.21489

Butler PM. 1963. Tooth morphology and primate evolution. Dental Anthropology. 5:1-14. Available

Butler PM. 1983. Evolution and mammalian dental morphology. Journal de Biologie Buccale. 11(4):285-302. Available from <Go to ISI>://A1983RY70500001

Crompton AW, Hiiemae K. 1970. Molar occlusion and mandibluar movements during occlusion in the American opposum, *Didelphis marsupialis*. Zoological Journal of the Linnaean Society. 49:21-47. Available

Cuozzo FP, Ungar PS, Sauther ML. 2012. Primate dental ecology: How teeth respond to the environment. American Journal of Physical Anthropology. 148(2):159-162. Available from http://www.ncbi.nlm.nih.gov/pubmed/22610891 doi 10.1002/ajpa.22082

Cuozzo FP, Head BR, Sauther ML, Ungar PS, O'Mara MT. 2014. Sources of tooth wear variation early in life among known aged wild ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve, Madagascar. American Journal of Primatology. Available

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. American Journal of Physical Anthropology. 125(2):152-161. Available from <Go to ISI>://000223933600005

Evans A, Fortelius M, Jernvall J. 2007. How does tooth wear affect dental complexity? Implications for tooth function and dietary reconstruction. Journal of Vertebrate Paleontology. 27(3):72a-72a. Available from <Go to ISI>://WOS:000249535400168

Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature. 445(7123):78-81. Available from <Go to ISI>://000243225100039

Evans AR, Jernvall J. 2009. Patterns and contraints in carnivoran and rodent dental complexity and tooth size. Journal of Vertebrate Paleontology. 29:24A. Available

Evans AR. 2013. Shape descriptors as ecometrics in dental ecology. Hystrix, the Italian Journal of Mammalogy. 24(1):133-140. Available

Fortelius M. 1985. Ungulate cheek teeth: Developmental, functional and evolutionary interrelations. Acta Zoologica Fennica. 180:1-76. Available

Fortelius M, Eronen JT, Kaya F, Tang H, Raia P, Puolamaki K. 2014. Evolution of Neogene Mammals in Eurasia: Environmental Forcing and Biotic Interactions. Annu Rev Earth Pl Sc. 42:579-604. Available from <Go to ISI>://WOS:000348436700025 doi 10.1146/annurev-earth-050212-124030

Fossey D, Harcourt AH. 1977. Feeding ecology of free ranging mountain gorillas. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. London: Academic Press. p. 415-447.

Friscia AR, Van Valkenburgh B, Biknevicius AR. 2007. An ecomorphological analysis of extant small carnivorans. Journal of Zoology. 272(1):82-100. Available from <Go to ISI>://000245745300010

Godfrey LR, Winchester JM, King SJ, Boyer DM, Jernvall J. 2012. Dental topography indicates ecological contraction of lemur communities. American Journal of Physical Anthropology. 148(2):215-227. Available from http://www.ncbi.nlm.nih.gov/pubmed/22610897 doi 10.1002/ajpa.21615

Herring SW. 1993. Functional morphology of mammalian mastication. Am Zool. 33(3):289-299. Available from <Go to ISI>://A1993LY61000001

Hiiemae KM. 1967. Masticatory function in mammals. Journal of Dental Research. 46(5P1S):883-893. Available from <Go to ISI>://A1967A102500018

Janis CM, Fortelius M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biological Reviews. 63:197-230. Available

Jernvall J, Hunter JP, Fortelius M. 1996. Molar tooth diversity, disparity, and ecology in cenozoic ungulate radiations. Science. 274(5292):1489-1492. Available from <Go to ISI>://A1996VV77500036

Karme A, Evans AR, Fortelius M. 2010. GISWear; 3D and GIS Diet Analysis Method for Bunodont Omnivore Groups Suina and Hominidae. Third International Palaeontological Congress (IPC3), London, Great Britain Abstract Volume. Available

Kay RF. 1975. Functional adaptations of primate molar teeth. American Journal of Physical Anthropology. 43(2):195-215. Available from <Go to ISI>://A1975AR63100005

Kay RF. 1977. Evolution of Molar Occlusion in Cercopithecidae and Early Catarrhines. American Journal of Physical Anthropology. 46(2):327-352. Available from <Go to ISI>://A1977CY74000012

Kay RF, Sussman RW, Tattersall I. 1978. Dietary and dental variations in genus *Lemur*, with comments concerning dietary-dental correlations among Malagasy primates

1. American Journal of Physical Anthropology. 49(1):119-127. Available from <Go to ISI>://A1978FF16200017

Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys and Apes. New York: Columbia University Press. p. 21-53.

Kay RF, Covert HH. 1984. Anatomy and behavior of extinct primates. In: Food Acquisition and Processing in Primates. New York: Plenum Press. p. 467-508.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. P Natl Acad Sci USA. 102:16579-16583. Available

Kinzey WG. 1978. Feeding behavior and molar features in two species of titi monkey. In: Recent Advances in Primatology, Volume 1, Behavior. New York: Academic Press. p. 373-385.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. The hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. American Journal of Physical Anthropology. 125:363-368. Available from <Go to ISI>://000079607500272

Ledogar JA, Winchester JM, St Clair EM, Boyer DM. 2013. Diet and dental topography in pitheciine seed predators. American Journal of Physical Anthropology. 150(1):107-121. Available from http://www.ncbi.nlm.nih.gov/pubmed/23212472 doi 10.1002/ajpa.22181

Liem KF. 1980. Adaptive significance of intraspecific and interspecific differences in the feeding repertoires of cichlid fishes. Am Zool. 20(1):295-314. Available from <Go to ISI>://WOS:A1980JN44100024

Liem KF, Kaufman LS. 1984. Intraspecific macroevolution: Functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In: Evolution of Species flocks. Orono, ME: University of Maine Press. p. 203-215.

Liu L, Puolamaki K, Eronen JT, Ataabadi MM, Hernesniemi E, Fortelius M. 2012. Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present. Proceedings of the Royal Society B: Biological Sciences. 279(1739):2793-2799. Available from http://www.ncbi.nlm.nih.gov/pubmed/22456884 doi 10.1098/rspb.2012.0211

Lucas PW. 2004. Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press.

M'Kirera F, Ungar PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. American Journal of Primatology. 60(2):31-41. Available from <Go to ISI>://000183959500001

McGraw WS. 2007. Positional behavior and habitat use of Taï monkeys. In: The Monkeys of the Tai Forest: An African Primate Community. Cambridge: Cambridge University Press. p. 223-255.

McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. American Journal of Physical Anthropology. 154(3):413-423. Available from <Go to ISI>://WOS:000337619200010 doi 10.1002/ajpa.22525

Mehlman PT. 2008. Current status of wild gorilla popuations and strategies for their conservation. In: Conservation in the 21st Century: Gorillas as a Case Study. New York: Springer Science. p. 3-54.

Meldrum DJ, Kay RF. 1997. *Nuciruptor rubricae*, a new pitheciin seed predator from the Miocene of Colombia. American Journal of Physical Anthropology. 102(3):407-427. Available from <Go to ISI>://A1997WR62900008

Norconk MA. 2007. Sakis, uakaris and titi monkeys: Behavioral diversity in a radiation of primate seed predators. In: Primates in Perspective. New York: Oxford University Press. p. 123-138.

Prinz JF, Silwood CJL, Claxson AWD, Grootveld M. 2003. Simulated digestion status of insects and insect larvae: A spectroscopic investigation. Folia Primatologica. 74(3):126-140. Available from <Go to ISI>://000183983100002

Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. American Naturalist. 151(3):223-235. Available from <Go to ISI>://000072128600002

Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. American Journal of Physical Anthropology. 45(2):281-297. Available from <Go to ISI>://A1976CE52700011

Rosenberger AL. 1992. Evolution of feeding niches in New World monkeys. American Journal of Physical Anthropology. 88(4):525-562. Available from <Go to ISI>://A1992JD59200007

Ross CF. 2000. Into the light: The origin of Anthropoidea. Annual Review of Anthropology. 29:147-194. Available from <Go to ISI>://000165670500010

Sanson GD. 1989. Morphological adaptations of teeth to diets and feeding in Macropodidae. In: Kangaroos, Wallabies and Rat-Kangaroos. Sydney, Australia: Surrey Beatty. p. 151-168.

Seligsohn D. 1977. Analysis of species-specific molar adaptations in strepsirhine primates. Contributions to Primatology. 11:1-116. Available

Seligsohn D, Szalay FS. 1978. Relationship between natural selection and dental morphology: Tooth function and diet in *Lepilemur* and *Hapalemur*. In: Development, Function and Evolution of Teeth. New York: Academic Press. p. 289-307.

Simpson GG. 1933. Paleobiology of Jurassic mammals. Paleobiologica. 5:127-158. Available

Strait SG. 1993. Differences in occlusal morphology and molar size in frugivores and faunivores. Journal of Human Evolution. 25(6):471-484. Available from <Go to ISI>://A1993MM55500002

Sussman RW. 1977. Feeding behavior in *Lemur catta* and *Lemur fulvus*. In: Primate Ecology: Studies in Feeding and Ranging Behavior in Lemurs, Monkeys and APes. London: Academic Press. p. 1-36.

Sussman RW. 1987. Morpho-physiological analysis of diets: species-specific dietary patterns in primates and human dietary adaptations. In: The Evolution of Human Behavior: Primate Models. Albany: SUNY Press. p. 157-179.

Teaford MF. 1983. The morphology and wear of the lingual notch in macaques and langurs. American Journal of Physical Anthropology. 60(1):7-14. Available from <Go to ISI>://A1983PY13700002

Teaford MF, Walker A. 1983. Dental microwear in adult and still-born guinea pigs (*Cavia porcellus*). Archive of Oral Biology. 28(11):1077-1081. Available from http://www.ncbi.nlm.nih.gov/pubmed/6581764

Turner AK. 1997. What's the difference among 2-D, 2.5-D, 3-D and 4-D? GIS World. 10(3):54. Available

Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. P Natl Acad Sci USA. 100(7):3874-3877. Available from <Go to ISI>://000182058400063

Ungar PS. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. Journal of Human Evolution. 46(5):605-622. Available from <Go to ISI>://000221427900005

Ungar PS. 2008. Materials science: Strong teeth, strong seeds. Nature. 452:703-705. Available

Ungar PS. 2009. Tooth form and function: Insights into adaptation through the analysis of dental microwear. In: Comparative Dental Morphology Basel: Karger Press. p. 38-43.

Ungar PS, Lucas PW. 2010. Tooth form and function in biological anthropology. In: A Companion to Biological Anthropology. Malden, MA: Wiley-Blackwell.

Ungar PS. 2015. Mammalian dental fucntion and wear: A review. Biosurface and Biotribology. 1:25-41. Available

Ungar PS. 2017. Primate ecology and dental-dietary adaptations: Foodprints for thought. In: Primate Diet and Nutrition. Chicago: University of Chicago Press.

Winchester JM, Boyer DM, St Clair EM, Gosselin-Ildari AD, Cooke SB, Ledogar JA. 2014. Dental topography of platyrrhines and prosimians: Convergence and contrasts. American Journal of Physical Anthropology. 153(1):29-44. Available from <Go to ISI>://000327898900004 doi Doi 10.1002/Ajpa.22398

Figure legends

Figure 1. Primary diet analyses. Principal Components Analyses for each of the three wear stages described in the text (left) and bivariate plots illustrating results for pairs of variables comparing groups by diet (right).

Figure 2. Secondary diet analyses for frugivores. Principal Components Analyses for each of the three wear stages described in the text (left) and bivariate plots illustrating results for pairs of variables comparing groups by diet (right).

Table 1. Specimens included in this study with diet attributions.

Taxon	n	Diet Primary	Secondary	References
Alouatta	60	leaves	fruit	Julliot and Sabatier, 1993
Alouatta belzebul	54			
Alouatta seniculus	6			
Aotus	9	fruit	insects	Wright, 1989
Aotus infulatus	9			
Ateles	32	fruit	seeds	Suarez, 2006
Ateles belzebuth	27			
Ateles paniscus	5			
Callicebus	35	fruit	leaves	
Callicebus moloch	35			
Callithrix	29	gums	insects	
Callithrix argentata	15			
Callithrix humeralifer	14			
Cebus	30	fruit	hard objects	Terborgh, 1983; Galetti and Padroni, 1994
Cebus apella	30			
Chiropotes	35	seeds	fruit	Van Roosmalen, 1981; ; Ayers, 1989
Chiropotes albinasus	14			
Chiropotes satanas	21			
Lagothrix	16	fruit	leaves	Defler and Defler, 1996
Lagothrix lagotricha	16			
Pithecia	19	seeds	fruit	Kinzey and Norconk, 1993; Peres, 1993
Pithecia irrorata	11			
Pithecia monachus	8			
Saguinas	41	fruit	insects	Anapol, 1994
Saguinas midas	41			
Saimiri	35	Fruit	insects	Terborgh, 1983; Lima and Ferrari, 2003
Saimiri ustus	35			

Table 2. Summary statistics. Individuals divided by diet and wear stage.

	n		Sharpness	Slope	Angularity	Relief	OPCR	ClumpSize
Wear stage 1								
Leaves/Fruit	18	Mean	0.253	40.345	88.904	178.385	64.972	10.955
		SD	0.029	2.975	0.189	15.982	7.89	2.226
Fruit/Insects	26	Mean	0.286	39.115	89.298	157.222	41.351	14.413
		SD	0.039	3.451	0.108	13.374	11.732	3.853
Fruit/Seeds	13	Mean	0.191	33.326	88.828	144.648	45.029	15.077
		SD	0.035	3.851	0.1	12.943	5.5	3.63
Fruit/Leaves	14	Mean	0.246	35.797	88.983	148.155	53.563	13.643
		SD	0.046	3.699	0.142	15.154	11.289	3.578
Gums/Insects	8	Mean	0.265	38.583	89.261	147.59	33.469	20.047
		SD	0.05	3.029	0.07	9.175	4.747	4.958
Seeds/Fruit	20	Mean	0.216	32.176	89.115	148.609	61.75	9.018
		SD	0.055	3.112	0.126	20.147	14.457	2.55
Fruit/Hard	8	Mean	0.211	33.462	88.725	138.835	42.688	20.031
		SD	0.045	3.415	0.102	6.203	5.892	5.717
Wear stage 2								
Leaves/Fruit	23	Mean	0.232	39.252	88.881	171.658	62.897	11.625
		SD	0.04	2.293	0.158	14.715	7.476	2.109
Fruit/Insects	27	Mean	0.306	39.528	89.318	158.17	42.065	14.141
		SD	0.053	4.186	0.123	17.316	11.154	3.651
Fruit/Seeds	11	Mean	0.176	29.436	88.818	133.271	43.886	17.233
		SD	0.049	3.101	0.049	7.641	7.58	5.34
Fruit/Leaves	28	Mean	0.23	32.99	88.996	142.314	54.045	12.071
		SD	0.049	4.272	0.136	15.672	14.18	2.334
Gums/Insects	5	Mean	0.259	37.475	89.374	145.598	36.1	20.712
		SD	0.026	1.892	0.055	6.451	2.42	1.684
Seeds/Fruit	17	Mean	0.172	28.585	88.992	137.558	56.919	9.018
		SD	0.035	3.422	0.15	14.147	14.744	2.55

Fruit/Hard	16	Mean	0.196	31.331	88.63	136.579	43.461	19.902
		SD	0.068	4.008	0.12	9.343	8.224	4.609
Wear stage 3								
Leaves/Fruit	18	Mean	0.21	35.67	88.908	165.352	66.729	14.413
		SD	0.033	2.682	0.118	16.666	8.462	3.853
Fruit/Insects	23	Mean	0.266	39.588	89.317	160.12	48.315	12.53
		SD	0.066	4.877	0.086	14.853	16.185	4.231
Fruit/Seeds	9	Mean	0.14	26.763	88.778	131.99	49.028	13.076
		SD	0.041	2.873	0.069	8.638	8.204	4.388
Fruit/Leaves	15	Mean	0.189	30.011	88.915	139.42	54.517	12.071
		SD	0.04	4.084	0.119	16.287	10.784	2.334
Gums/Insects	15	Mean	0.268	37.405	89.295	146.391	38.333	16.104
		SD	0.055	4.256	0.08	11.029	11.452	4.616
Seeds/Fruit	17	Mean	0.141	25.986	88.914	130.347	51.669	9.566
		SD	0.021	3.556	0.141	10.267	9.911	2.728
Fruit/Hard	8	Mean	0.174	30.762	88.624	146.665	42	18.484
		SD	0.047	5.124	0.173	29.589	5.919	3.819

Table 3. Principal Components Analysis results.

Component	1	2	3	4	5
Percent variance explained	44.956	30.064	13.756	5.660	4.276
Variance by components	2.697	1.804	0.825	0.340	0.257
Sharpness	0.839	0.255	-0.087	0.460	-0.095
Slope	0.945	0.038	0.229	-0.093	0.012
Angularity	0.672	0.046	-0.691	-0.180	0.190
Relief	0.805	-0.329	0.405	-0.220	-0.065
OPCR	0.000	-0.918	0.124	0.198	0.319

Table 4. MANOVA/ANOVA and multiple comparisons tests with specimens grouped by primary diet preference. ANOVA and

	ANOVA results							Wilks' λ	
	Sharpness	Slope	Angularity	Relief	OPCR	Clump size	*df*	*F*	*df*
Primary	19.363*	41.244*	17.707*	43.489*	65.763*	65.65*	3, 327	35.727*	18, 911
Wear	9.606*	9.738*	0.991	4.944*	0.153	3.858*	2, 327	3.343*	12, 644
Interaction	1.457	1.118	1.087	1.435	1.567	1.433	6, 327	1.667*	36, 1416

	Pairwise comparisons					
Primary	Sharpness	Slope	Angularity	Relief	OPCR	Clump size

Wilks' λ results *$p < 0.05$, pairwise comparisons **$p < 0.05$ Tukey's and Fisher's tests, *$p < 0.05$ Fisher's test only.

fruits x gums	-51.662**	-55.359**	-109.812**	-5.578	82.915**	-56.42**
fruit x leaves	-0.558	-69.247**	49.047**	-116.95**	-131.475**	80.811**
fruits x seeds	86.244**	92.918**	3.859	49.694**	-71.508**	139.44**
gums x leaves	51.104*	-13.888	158.859**	-111.372**	-214.39**	137.231**
gums x seeds	137.906**	148.276**	113.671**	55.271**	-154.423**	195.86**
leaves x seeds	86.803**	162.164**	-45.188**	166.643**	59.968**	58.629**

Table 5. MANOVA/ANOVA and multiple comparisons tests with frugivores grouped by secondary diet. ANOVA and Wilks' λ results *$p < 0.05$, pairwise comparisons **$p < 0.05$ Tukey's and Fisher's tests, *$p < 0.05$ Fisher's test only.

	ANOVA results						Wilks' λ		
	Sharpness	Slope	Angularity	Relief	OPCR	Clump size	*df*	*F*	*df*
Secondary	53.872*	61.74*	287.873*	34.37*	12.086*	14.901*	3, 186	31.929	8, 512
Wear	10.346*	9.743*	1.618	3.093*	1.28	3.698*	2, 186	3.852	12, 362
Interaction	n/a	n/a	n/a	n/a	n/a	n/a	6, 186	1.059	36, 797

Secondary	Sharpness	Slope	Angularity	Relief	OPCR	Clump size
hard x insects	-78.778**	-78.599**	-135.954**	-73.214**	-6.336	66.303**
hard x leaves	-26.133**	-11.673	-65.467**	-15.293	-57.682**	74.333**
hard x seeds	17.505	15.928	-30.564**	4.903	-20.027	48.909**
insects x leaves	52.645**	66.925**	70.487**	57.921**	-51.346**	8.031
insects x seeds	96.283**	94.527**	105.39**	78.117**	-13.691	-17.394
leaves x seeds	43.638**	27.601**	34.903**	20.196	37.656**	-25.424*

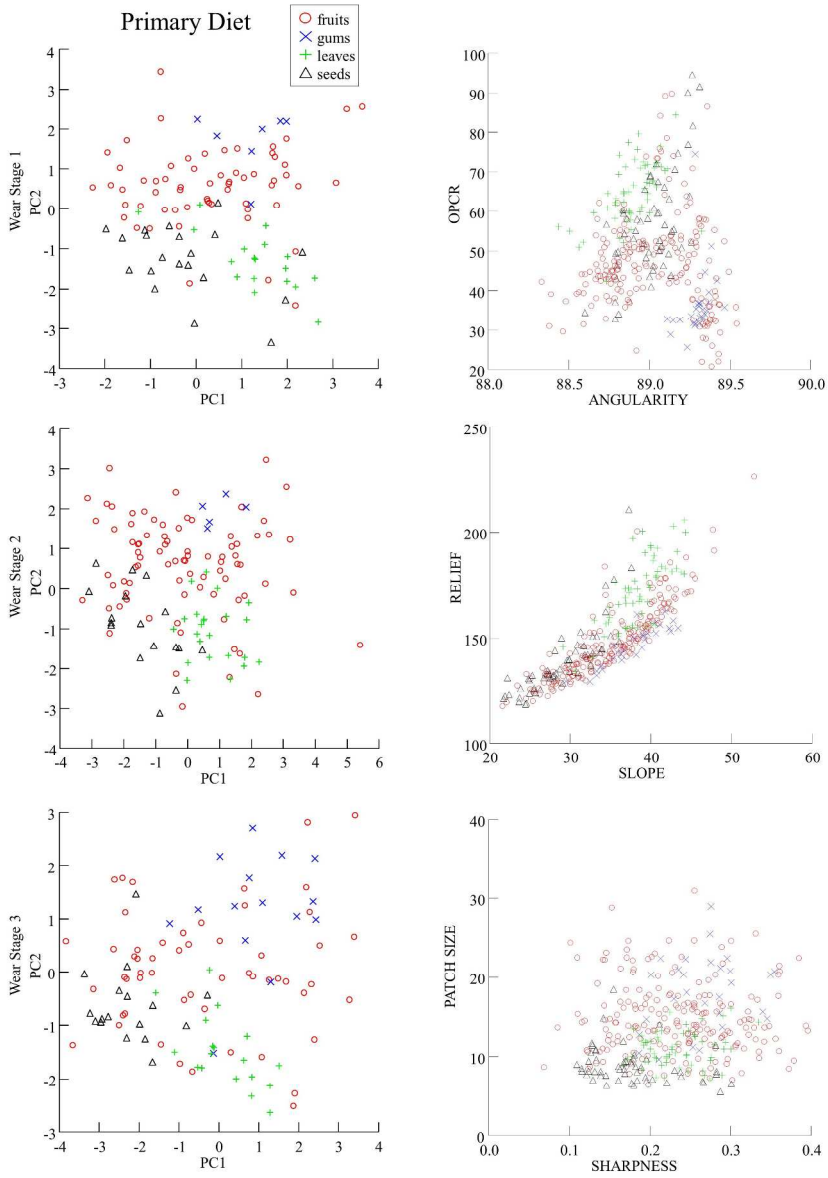

Figure 1. Primary diet analyses. Principal Components Analyses for each of the three wear stages described in the text (left) and bivariate plots illustrating results for pairs of variables comparing groups by diet (right).
762x1016mm (96 x 96 DPI)

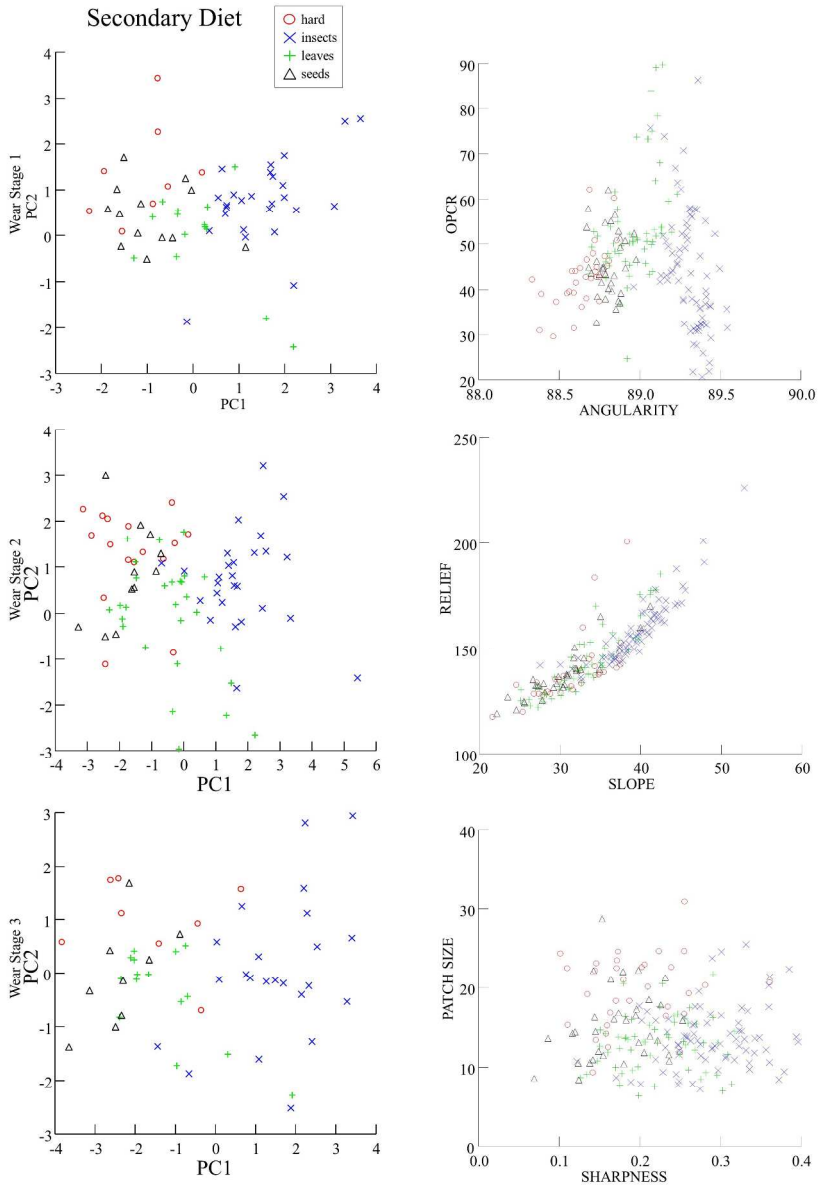

Figure 2. Secondary diet analyses for frugivores. Principal Components Analyses for each of the three wear stages described in the text (left) and bivariate plots illustrating results for pairs of variables comparing groups by diet (right).
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